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CROTALUS MITCHELLII, THE SPECKLED RATTLESNAKE

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INTRODUCTION

Crotalus mitchellii, a rattlesnake of the southwestern United States and Lower California, is characterized by great variability of head scalation, pattern, and color. This morphological plasticity has rendered the determination of its status and relationships somewhat difficult. It is the purpose of this paper to present the results of a reinvestigation of the form, largely based on specimens lately acquired; especially worthy of mention is a series from the Cape region of Lower California, the first available from that area in sufficient numbers to permit a statistical analysis.

HISTORICAL

Crotalus mitchellii was first described by Cope in 1861^1 as Caudisona Mitchellii, based on a specimen (USNM $5291\frac{1}{2}$) collected by John Xantus at Cape St. (San) Lucas, Lower California. The snake was named in honor of Dr. S. Weir Mitchell, the famous Philadelphia neurologist, scientist, and author, who was at that time engaged in researches on rattlesnake venoms. In 1866^2 Cope described as Caudisona pyrrha a specimen (USNM 6606) collected by Dr. Elliott Coues at Canyon Prieto, near Fort Whipple, Yavapai County, Arizona.³ Cope recognized the affinity of this new form with mitchellii.

Writing in 1893 (published in 1895) Stejneger⁴ considered *pyrrhus* a subspecies of *mitchellii*. In 1894, with new material available from Lower California, Van Denburgh⁵ showed that the differences which

¹ Proc. Acad. Nat. Sci. Phila., 1861, p. 293.

² Proc. Acad. Nat. Sci. Phila., 1866, p. 308.

³ A graphic contrast between the difficulties faced by the collectors of the past, as compared with the facilities of the present, is afforded by Coues' reference to this specimen: "It is not in the best order, as it was procured under the untoward circumstances of a hasty retreat from hostile Indians."

⁴ Rept. U. S. Nat. Mus. for 1893, 1895, p. 456.

⁵ Proc. Cal. Acad. Sci., Ser. 2, Vol. 4, p. 450.

Cope had used to segregate *pyrrhus* from *mitchellii* failed to hold in a larger series; he therefore placed *pyrrhus* in the synonymy of *mitchellii*, where it has since remained.

A closely allied species, *Crotalus tigris*, must now be surveyed; this was first described by Kennicott from southern Arizona in 1859.⁶ In reporting the results of the Death Valley Expedition, Stejneger⁷ classified, as belonging to this species, certain rattlesnakes collected in east-central California and southern Nevada. In 1929 Amaral,⁸ noting the similarity of this California-Nevada material with *mitchellii*, considered the latter a subspecies of *tigris*.

The present writer⁹ reviewed the situation in 1930 and reached the conclusion that these California-Nevada snakes were different from the true Arizona *tigris*. Noting border-line specimens from Mineral and Esmeralda Counties, Nevada, which showed certain affinities to *Crotalus confluentus lutosus*, I considered these as coming within the *confluentus* group, and applied to the snakes from California and Nevada, formerly considered *tigris*, the name *Crotalus confluentus stephensi*. As the relationship between this form and *mitchellii* was evident, the latter became *Crotalus confluentus mitchellii*.

This classification led to a curious anomaly, namely, the presence of two subspecies in the same territory without intergradation, for, in southern California, *Crotalus confluentus oreganus* and *C. c. mitchellii* occupy extensive areas together. Of the ring *oreganus-lutosus-stephensimitchellii* connecting these forms, clearly the *lutosus-stephensi* link was the weakest. With the considerable additional material that has come to hand I am now inclined to the belief that the Mineral-Esmeralda (Nevada) specimens are pure *stephensi*, rather than *lutosus-stephensi* intergrades.

Gradually new material, especially in the Museum of Vertebrate Zoology, has brought the *lutosus* and *stephensi* ranges together in other areas and this without any approach toward intergradation; that is, the border specimens of one species do not show a tendency toward the other form, each retaining its individuality. While an actual overlap in ranges has not yet been shown, thus finally settling the *lutosus-stephensi* nonintergradation beyond question, still such an overlap is indicated as

⁶ Rept. U. S. Mex. Boundary Survey, Vol. 2, 1859, p. 14.

⁷ North American Fauna, No. 7, 1893, p. 214.

⁸ Bull. Antivenin Inst. Am., Vol. 2, 1929, p. 82.

⁹ Trans. S. D. Soc. Nat. Hist., Vol. 6, No. 3, 1930, p. 95.

probable, particularly in the Belted Range in Nevada. Thus it is my present conclusion that *mitchellii* (and with it *stephensi*) should be divorced from the *confluentus* group.

At the same time the augmented collections of the past four years from other areas, particularly the large series from the Cape region of Lower California, together with a study of additional characters, have convinced me that these Cape specimens are different in several particulars, especially head size and rattles, from those found in Arizona and California and therefore *pyrrhus* should be revived as the subspecific name for the latter form.

Concerning the relationship of the *mitchellii* group with *tigris* I have not changed my previously expressed opinions.¹⁰ While *mitchellii* (especially as exemplified by the Cape subspecies) is closely allied to *tigris*, there is an actual overlap of the ranges of the two species, without intergradation, in central Arizona. *Tigris* is a species which, as far as now known, is restricted to central and southern Arizona, and Sonora; its differences from *stephensi* are quite definite and consistent.

Thus at present I view *mitchellii* as comprising three subspecies as follows:

- Crotalus mitchellii mitchellii: Cape and central areas of Baja California.
- Crotalus mitchellii pyrrhus: Central and southwestern Arizona; the Californias from central San Bernardino County south to the Sierra San Pedro Mártir of Baja California.
- Crotalus mitchellii stephensi: Cailfornia, east of the Sierras from Inyo County south to central San Bernardino County; southwestern Nevada.

In the outline which follows there are presented first, descriptions of these forms, their ranges and morphology, followed by a discussion of the characters in which they differ from, or resemble, each other and closely allied species. In these data advantage is taken of the enlarged collections now available and of studies of variation which have been made preparatory to a general summary of rattlesnake characters.

Mitchellii is a peculiar snake in that a tendency to subdivision of its head scales renders their classification difficult; also it is, amongst all the rattlesnakes, the most variable in color and pattern. The separation

¹⁰ Trans. S. D. Soc. Nat. Hist., Vol. 6, No. 3, 1930, p. 106; *ibid*. Vol. 6, No. 24, 1931, p. 353.

of the rostral from the prenasals by a row of granules or small scales, long thought to be a simple and universal criterion of *mitchellii*, is not always present in this form, even if we omit the subspecies *stephensi* from consideration; also this separation sometimes occurs in certain other species, notably *C. c. oreganus* from Arizona. Thus a simple and invariable key character for this group is not available.

Mitchellii has often been called the White, Bleached, or Faded Rattlesnake, especially based on specimens from southwestern Arizona, which happen to have been among the first to be brought east alive. But from many sections it is brightly colored and strongly, although indefinitely, patterned. I deem it best to refer to the two more typical subspecies as Speckled Rattlesnakes, for the punctations which constitute the pattern are its most outstanding characteristic.

Crotalus mitchellii mitchellii (Cope)

SAN LUCAN SPECKLED RATTLESNAKE

Plate 19, fig. 1

- 1861 Caudisona Mitchellii Cope, Proc. Acad. Nat. Sci. Phila., 1861, p. 293. (Type locality: Cape St. (= San) Lucas, Lower California, Mexico. Type specimen: USNM 5291¹/₂¹¹ collected by John Xantus.)
- 1875 Crotalus mitchellii Cope, in Yarrow Surv. W. 100th Merid., Vol. 5, p. 535.
- 1882 Crotalus mitchelli Yarrow, Bull. U. S. Nat. Mus., No. 24, pp. 12, 73.
- 1883 Crotalus oreganus var. mitchelli Garman, Mem. Mus. Comp. Zoöl., Cambr., Vol. 8, No. 3, p. 173.
- 1887 Crotalus mitcheli Belding, West American Scientist, Vol. 3, No. 24, p. 98.
- 1887 Crotalus mitchillii Cope, Bull. U. S. Nat. Mus., No. 32, p. 90.
- 1894 Crotalus mitchellii (part) Van Denburgh, Proc. Cal. Acad. Sci., Ser. 2, Vol. 4, p. 450.
- 1895 Crotalus Mitchellii Mitchellii Stejneger, Rept. U. S. Nat. Mus. for 1893. p. 454.
- 1929 Crotalus tigris mitchellii (part) Amaral, Bull. Antivenin Inst. Am., Vol. 2, No. 4, p. 82.
- 1930 Crotalus confluentus mitchellii (part) Klauber, Trans. S. D. Soc. Nat. Hist., Vol. 6, No. 3, p. 108.

Material.—Of this subspecies 81 specimens from the Cape region of Baja California have been available for study, of which fifty were seen alive. In addi-

¹¹ This specimen has apparently disappeared; in fact, Dr. Stejneger says it had been removed from the USNM collection before his coming to the museum fifty years ago. It has not been located amongst the Cope material in the collection of the Academy of Natural Sciences of Philadelphia.

tion there are 5 specimens from three different Gulf of California islands; the latter however are omitted from the descriptive summary as it is not desired to complicate the statistics with possible incipient island subspecies. No specimens are available to me from the central area of the peninsula (the vicinity of Mulegé, Santa Rosalia, and San Ignacio). There are five specimens in the Paris Museum from this area; of these Mr. F. Angel has kindly supplied me the measurements. These indicate that the speckled rattlesnakes of that vicinity, while intermediate between C. mitchellii mitchellii and C. m. pyrrhus, are somewhat closer to the former, so they have been included therewith. The affiliation is not unexpected, for in many kinds of reptiles the Cape species extend to the central area with a break between these and the San Diegan forms further to the north. Thus in the present instance we consider C. m. mitchellii to extend as far north as San Ignacio. The most southerly available specimen of pyrrhus is from the Sierra San Pedro Mártir;¹² we assume that, in this gap of about 250 miles, intergradation, which is begun in the San Ignacio area will be found complete, for this intervening territory is of a character suitable to C. mitchellii.

Range.—*C. m. mitchellii* has been collected at the following localities in the southern and central areas of Lower California, and adjacent islands on the Gulf of California and Pacific coasts. (See map). For a few localities approximate latitudes are given where the identity, through duplication of names or obscurity, may be confusing.

Cape San Lucas (Type locality)	San Evaristo (24°50′)
San José del Cabo	Santo Domingo (25°30')
Sierra El Taste	Punta Escondido (25°50')
Sierra San Lazaro	Mulegé
Miraflores	Santa Rosalía
Todos Santos (23°30')	San Ignacio
La Rivera (Riberia)	Ceralvo Island
Agua Caliente (23°30')	Espiritu Santo Island
Ensenada de los Muertos (24°)	San José Island
La Paz	Santa Margarita Island

Lepidosis and Form.—Size medium among rattlesnakes. Scale rows at midbody usually 25 (90 per cent), rarely 23 (6 per cent) or 27 (4 per cent). The scales are strongly keeled, except the first row on each side. Scale bosses are rather conspicuous. Ventrals: males, (52 specimens) max. 181, min. 165, av. 176.69 \pm 0.32 interquartile range 174.4—179.0, coefficient of variation 2.0 per cent; females, (27 specimens) max. 186, min. 172, av. 179.44 \pm 0.45, interquartile range 177.1—181.8, coefficient of variation 1.9 per cent. Anal entire. Caudals: males 28 to 22, average of 44 specimens 25.1 \pm 0.12; females 23 to 16, average of 27 specimens 20.7 \pm 0.21. The caudals, while generally entire, may have a few at either end of the series divided.

The supralabials usually number 15 (24 per cent), 16 (49 per cent), or 17

¹² An intermediate specimen from Las Huevitas (sometimes given as Huavitas or Cuevitas) near San Fernando Mission, contained in the California Academy of Sciences collection, was destroyed in the fire of 1906.

(16 per cent); occasionally 14 (4 per cent) or 18 (6 per cent); rarely 13 or 19 (less than 1 per cent of each). The infralabials generally number 15 (39 per cent) or 16 (37 per cent); occasionally 14 (10 per cent) or 17 (13 per cent); rarely 13 (less than 1 per cent). The posterior supralabials are often divided horizontally, thus being lower than the scales next above.

The rostral is usually wider than high, as is characteristic of this species; however in 10 per cent the width and height are equal and in 7 per cent it is higher than wide. As is usually the case with this species the prenasals are separated from the rostral by rows of scales or granules; only 3 per cent make contact.

The prenasals are also usually separated from the supralabials by the extension to the rostral of the small scales anterior to the pit; this separation is evident in 83 per cent of the specimens examined. The internasals cannot be counted with accuracy as they form part of the row of scales which, continued down along the sides of the rostral, separate that scale from the prenasal. In fact this tendency, which is so characteristic of *mitchellii*, of splitting such scales as the prenasals, loreals, canthals, and preoculars, renders a statistical analysis of the head scales difficult and to some extent useless. Therefore, only the more important items are cited.

The scales on the crown anterior to the supraoculars vary from 25 to 46, interquartile range 31.5 to 37.9, average 34.7. The minimum scale rows between supraoculars vary from 1 to 8, interquartile range 4.7—6.3, with an average of 5.5.

Supraocular sutures or indentations are present in only 3 per cent of the specimens. The nasals are 2—2. About 60 per cent of the specimens have two loreals, the rest from 1 to 4. The scales along the canthus rostralis from rostral to supraocular usually number from 5 to 7.

The upper preocular is frequently split horizontally, vertically, or both; there results confusion with both loreals and canthals so that the classification of these scales and the determination of their contacts, useful in the classification of some species, is here usually impossible. There is often a small, circular scale between the two preoculars; this is quite characteristic of this subspecies, but is not invariably present.

The scale rows from labials to orbit usually number 3 or 4; the scales in the orbital ring average about 9.

The first infralabials are undivided; normally, 2 or 3 are in contact with the genials on each side.

The mental is triangular. The genials are in a single pair, relatively short and obtuse. Intergenials are present in only one per cent of the specimens and submentals in 2 per cent.

In shape the head is subtriangular and depressed, as compared with most rattlesnake species. The average ratio of body length to head length in adults (over 700 mm. in length) is 24.6. The ratio of the distance across the supraoculars to the space between averages 2.5.

The average ratio of the length of tail to total length exclusive of rattle is 0.080 in adult males and 0.063 in females.

The largest specimen examined measured 958 mm. (39 in.) when alive.

Color and Pattern.—This snake is light-gray or tan in ground color with a dorsal series of large and highly irregular blotches which almost obscure the ground.

The blotches are neither clearly outlined nor of regular form; they consist partly of darker scales, but more conspicuously of large aggregations of black or dark-brown punctations. The blotch centers are usually somewhat lighter than the edges. Toward the tail the blotches become rings. Secondary and, occasionally, tertiary series of blotches are in evidence on the sides. The inter-blotch light areas are freest of punctations along the mid-dorsal line, but even here the ground color is seldom spotless. As a result, the live snake usually gives the impression of a quiet, gray or brown neutrality. The extreme color variations found in *pyrrhus* in California and Arizona do not seem to be present in this southern race. Below, the color is buff, with aggregations of dark spots.

The head is spotted but is neither conspicuously nor regularly marked. There is a dark line from the eye to a point above the angle of the mouth. The outer edge of each supraocular usually has a conspicuous, light tip.

The tail rings are alternating ash-gray and black, in some contrast to the rest of the body. The light are usually wider than the dark rings, thus following *scutulatus* rather than *atrox*.

In number the body blotches vary from 26 to 39, the average being 31.7 ± 0.23 in the males and 32.0 ± 0.36 in the females. The coefficient of variation is about 8 per cent in this characteristic.

The tail rings number 3 to 5 in the males, with an average of 3.8 ± 0.06 , and 3 or 4 in the females (average 3.2 ± 0.05).

Crotalus mitchellii pyrrhus (Cope)

SOUTHWESTERN SPECKLED RATTLESNAKE

Plate 19, fig. 2 and Plate 20, fig. 1

- 1866 Caudisona pyrrha Cope, Proc. Acad. Nat. Sci. Phila., 1866, p. 308. (Type locality: Canyon Prieto, Yavapai County, Ariz. Type specimen: USNM 6606 collected by Dr. E. Coues).
- 1875 Crotalus pyrrhus Cope, in Yarrow, Surv. W. of 100th Merid., Vol. 5, p. 535.
- 1883 Crotalus confluentus var. pyrrhus Garman, Mem. Mus. Comp. Zoöl., Cambr., Vol. 8, No. 3, p. 173.
- 1894 *Crotalus mitchellii* (part) Van Denburgh, Proc. Cal. Acad. Sci., Ser. 2, Vol. 4, p. 450.
- 1895 Crotalus Mitchellii pyrrhus Stejneger, Rept. U. S. Nat. Mus. for 1893, p. 456.
- 1896 Crotalus mitchelli (part) Boulenger, Cat. Snakes, Brit. Mus., Vol. 3, p. 580.
- 1922 Crotalus goldmani Schmidt, Bull. Am. Mus. Nat. Hist., Vol. 46, Art. 11, p. 701. (Type locality: El Piñon, 5300 ft., San Pedro Mártir Mts., Lower California. Type specimen: USNM 37573 collected by Nelson and Goldman).

- 1929 Crotalus tigris mitchellii (part) Amaral, Bull. Antivenin Inst. Am., Vol. 2, No. 4, p. 82.
- 1930 Crotalus confluentus mitchellii (part) Klauber, Trans. S. D. Soc. Nat. Hist., Vol. 6, No. 3, p. 108.

Material.—I have had a considerable field and reptile-house experience with this form, particularly in southern California, and have seen in excess of four hundred live specimens. The following preserved specimens have been available for study:

Arizona:		
Yavapai County	14	
Maricopa County	7	
Yuma County	3	
Mohave County	3	27
California:		
San Bernardino County	21	
Riverside County	14	
Imperial County	8	
San Diego County	96	139
Northern Lower California:		13
Angel de la Guarda Island:		5
Unknown		1
	Total	185

Range.—*C. m. pyrrhus* is extensively distributed in rocky situations in central and western Arizona, southern California, and northern Lower California. (See map). It is certainly present but has not yet been recorded in northwestern Sonora. The known localities of collection are as follows:

Ari	ZONA
Yavapai County:	Yuma County:
Canyon Prieto, near Ft. Whipple	Mohawk Mts.
(Type locality)	Tule Mts.
Drake	Tinajas Altas Mts.
Hillside	Gila Mts.
Date Creek	Gonzales Well
Congress Junction	20 mi. N. of Picacho
MARICOPA COUNTY:	5 mi. N. of Mohawk, near
Wickenburg	Gila River
8 mi. SE. of Wickenburg	Mohave County:
Hot Springs Junction	2 mi. SW. of Valentine
Cave Ćreek	Chemehuevis Mts.
Black Canyon, 25 mi. N. of	Foot of The Needles
Phoenix	Topock
Estrella Mts.	*
Mts. S. of Phoenix	
Near Phoenix	

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SAN BERNARDINO COUNTY: 3 mi. N. of Topock Bridge Beal Klinefelter Mountain Spring (N. end Piute Mts.) 14 mi. NE. of Blythe Junction Gilroy Canyon, Providence Mts. Turtle Mts. Twentynine Palms Key's Ranch Windmill Tank Old Woman Spring 9 mi. S. of Old Woman Spring Cushenbury Spring Cushenbury Grade Bet. Cushenbury Spring and Lake Baldwin Johnston Ranch below Lake Baldwin Forest Home Lucerne Valley Deadman's Point 12 mi. S. of Barstow Oro Grande Victorville **RIVERSIDE COUNTY:** Palen Mts. 10 mi. N. of Desert Center 6 mi. SW. of Shaver's Well 5 mi. E. of Mecca 1 mi. S. of Indian Wells Palm Springs Murray Canyon near Palm Canyon Mouth San Andreas Canyon Whitewater Santa Rosa Mts. Coahuila Mt. Nightingale Ranch Ribbonwood Asbestos Spring Poppet Flat Vanderventer Flat Pinyon Flat Banning

CALIFORNIA RIVERSIDE COUNTY (continued): Schain's Ranch Road, 5 mi. W. of Banning Between Idyllwild and Keen Camp S. Fork, San Jacinto River Hemet Temescal Canyon San Juan Canyon, Elsinore Mts. 5 mi. E. of San Juan Hot Springs **ORANGE COUNTY:** 3 mi. E. of Hot Springs in Elsinore Mts. IMPERIAL COUNTY: Near Picacho Near Seeley Coyote Wells Myers' Creek Bridge Mountain Spring Boulder Park SAN DIEGO COUNTY: Point Loma Mission Valley Fallbrook Pala Escondido Mission Gorge Lakeside El Monte Lakeview (Johnstown) El Cajon Dehesa Rincon Warners Ranch Valley Center Lake Wohlford Sutherland Santa Ysabel Ramona San Vicente Wildwood Shady Dell Padre Barona El Capitan Dam Mussey Boulder Creek

SAN DIEGO COUNTY (continued):
Palomar Mt.
Cuyamaca Mt.
Laguna Mt.
Laguna Junction
Coyote Canyon
Collins Valley
Culp Valley
Borego Palm Canyon
Tubbs' Spring
San Felipe Valley
Sentenac Canyon
La Puerta (Mason Valley)
Grapevine Spring
Yaqui Well
The Narrows
Vallecito
Boulevard
Jacumba
Carrizo Gorge
Near Mountain Spring
Dos Cabezas

There are, in the literature, two Los Angeles County records, namely, Fairmont and Lovejoy Springs. It is not improbable that these are the results of inaccurate identifications, particularly the former, and therefore they are not regularly listed above.

BAJA CALIFORNIA

East Base, Cocopah Mts. Volcano Lake Garcia (S. D. & A. Ry.) Redondo (S. D. & A. Ry.) Tecate 8 mi. E. of Valentín 4 mi. N. of San Pedro (32°5') Laguna Hanson Descanso (32°15') San Antonio (near Socorro) San Matias (31°15') San José (31°) Parral (30°40') El Piñon, San Pedro Mártir Mts. (Type locality of goldmani). Las Huevitas (Lat. 30°) Angel de la Guarda Island

Lepidosis and Form.—Size large among rattlesnakes. Scale rows at midbody usually 25 (71 per cent), occasionally 23 (19 per cent), or 27 (10 per cent). The scales are strongly keeled, except the first row on each side. Ventrals: males (110 specimens), max. 185, min. 168, av. 177.56 \pm 0.21, interquartile range 175.3 —179.8, coefficient of variation 1.9 per cent; females (53 specimens), max. 187, min. 163 (170 if one aberrant specimen be omitted), av. 179.25 \pm 0.39, interquartile range 176.4—182.1, coefficient of variation 2.3 per cent. Anal entire. Caudals: males 28 to 20, average of 110 specimens 23.7 \pm 0.10; females 23 to 16, average of 51 specimens 19.1 \pm 0.17. The caudals, while generally entire, may have a few at either end of the series divided.

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The supralabials vary from 13 to 19; they usually number 15 (25 per cent), 16 (36 per cent), or 17 (27 per cent); occasionally 14 (5 per cent) or 18 (6 per cent); rarely 13 or 19 (less than 1 per cent of each). The infralabials generally number 15 (20 per cent), 16 (39 per cent), or 17 (26 per cent); occasionally 14 (7 per cent) or 18 (6 per cent); rarely 13 or 19 (less than 1 per cent of each).

The rostral is usually wider than high; however, this is by no means the important characteristic it has been often assumed, since 18 per cent of the specimens examined were higher than wide and 30 per cent were equal in the two dimensions. The prenasals are normally not in contact with the rostral, this lack of contact being highly characteristic of the present species. However, in 6 per cent of the specimens examined, contact is made on one side and in 12 per cent on both; thus 82 per cent run true to form, but in the others this key character partly or entirely fails. The prenasals are in contact with the supralabials in 24 per cent of the cases; the contact is entirely prevented in 32 per cent by the extension to the rostral of the small scales anterior to the pit, and the contact is partly prevented by these same scales in the remaining 44 per cent. The internasals are indeterminate since the nasals do not ordinarily contact the rostral.

The scales on the crown anterior to the supraoculars number at least 21 and average about 35. The minimum scale rows between supraoculars vary from 4 to 8, interquartile range 5.2–6.5, average 5.9.

Sutures or indentations are present in 9.3 per cent of the supraoculars. The nasals are 2-2. The loreals are often identified with difficulty; they vary from 0 to 4, with an average of about 1.5.

The upper preocular is frequently split, horizontally, vertically, or both; in fact, in only 28 per cent of the cases is it entirely intact, and in no less than 34 per cent is split in both directions.

The scale rows from labials to orbit usually number from 2 to 4. There are from 7 to 12 scales in the orbital ring, most specimens having 8 or 9.

The first infralabials are often divided (22 per cent divided, 78 per cent undivided).

The mental is triangular. The genials are in a single pair, relatively short and obtuse. Intergenials are present in 7.8 per cent of the specimens; submentals in only 1.4 per cent.

In shape the head is subtriangular, and depressed as compared with most species of the genus. The average ratio of body length to head length in adults (over 700 mm. in length) is 21.5.

The ratio of the length of tail to total length exclusive of rattle is approximately 0.072 in adult males, and 0.057 in females.

The largest specimen examined measured 1295 mm. (51 in.); the smallest 303 mm. (12 in.).

Color and Pattern.—This is the most variable of all the rattlesnakes in color and pattern; its bewildering variety renders any considerable accuracy or consistency of description quite impossible.

The ground color may be white, cream, tan, buff, drab, gray, brown, pink, orange, or salmon. On this there is superimposed a series of blotches which may approach hexagons, hour-glasses (with transverse axes), diamonds, rectangles, or cross-rings. The blotches consist partly of dark-colored scales and partly of dark punctations; these two forms of color application may blend or be in strong contrast. The blotches may be pink, salmon, red, brown, gray, black, or mixtures of these. They are usually highly irregular and indefinite in outline. There is also present a secondary series of blotches on each side; these may be of the same or twice the frequency of the main series. Caudad the two series are confluent to form transverse rings. A tertiary series is sometimes present.

The ground color is usually freest from punctations along the mid-dorsal line; along the sides gray punctations and even a gray suffusion are likely to be present, this being particularly the case with Mohave Desert specimens toward the *stephensi* range. Black scale tips are often present as in *stephensi*. Sometimes the blotches have light centers. The lower surfaces are cream, buff, or pink, usually blotched or punctated. The head is irregularly blotched or spotted. A postocular dark line is sometimes present. Supraocular light cross-dashes or light outer edges are often in evidence.

The tail rings are frequently in considerable color contrast with the body blotches, the terminal rings being usually black, even though the body be pink. An ash-gray ground color on the tail, of the *atrox* and *scutulatus* type, may be present.

In some areas this snake maintains a rather consistent coloration. Thus, in Yavapai County, Arizona, from Wickenburg north it is almost invariably a beautiful pink or salmon-red, a color which, by-the-way, fades badly in preservation, so that these snakes must be seen alive to observe the full effect. Pink, however, is not a universal Arizona coloration, since the mountains to the south of Phoenix produce light grayish-green specimens, while those from the Yuma sector are tan. In the Elsinore Mountains of Orange and Riverside counties, California, there is found a color variety in a beautiful shade of orange, with blotches of burntorange. In some sections of the Mohave Desert the snakes are russet-brown.

The lightest specimens I have seen came from the Tinajas Altas Mts., Yuma County, Arizona. In these the ground color is creamy-white; individuals from this area originally caused *mitchellii* to be known as the "White Rattlesnake." (Plate 20, fig. 1). It is said that these snakes blend well with a white granite found in that vicinity.

However, that these color varieties are not always territorially consistent is shown by the snakes of San Diego County, where, although grays and browns predominate, pink, salmon-red, and buff individuals are also present. Occasionally specimens are found with black scales or blotches on a light-gray ground; this form has locally been well termed the "granite rattler."

The body blotches number from 23 to 42, the average for the males being 33.7 ± 0.18 and for the females 32.9 ± 0.28 . The tail rings average 5.6 ± 0.06 in the males (range 4 to 9), and 4.4 ± 0.08 in the females (range 3 to 6).

Crotalus mitchellii stephensi Klauber

PANAMINT RATTLESNAKE

Plate 20, fig. 2.

1893 Crotalus tigris Stejneger, North American Fauna, No. 7, p. 214.

1896 Crotalus tigris (part) Boulenger, Cat. Snakes Brit. Mus., Vol. 3, p. 580.

- 1929 Crotalus tigris tigris (part) Amaral, Bull. Antivenin Inst. Am., Vol. 2, No. 4, p. 82.
- 1930 Crotalus confluentus stephensi Klauber, Trans. S. D. Soc. Nat. Hist., Vol. 6, No. 3, p. 108. (Type locality: 2 mi. W. of Jackass Springs, 6200 ft., Panamint Mts., Inyo County, Calif. Type specimen: MVZ 6699 collected by Dr. Jos. Grinnell).
- 1933 Crotalus mitchellii (part) Stejneger and Barbour, Check List N. A. Amph. and Repts., 3d Ed., p. 136.

Material.—Of this subspecies there have been available for study, the following:

INEVADA:		
Mineral County	1	
Esmeralda County	6	
Nye County	6	
Clark County	3	16
· · · · · · · · · · · · · · · · · · ·		
California:		
Mono County	1	
Inyo County	43	
Kern County	1	
San Bernardino County	5	50
· · · · · · · · · · · · · · · · · · ·		

TOTAL

About thirty individuals of this form have been seen alive.

Range.—C. m. stephensi is an inhabitant of the desert-mountain region lying east of the crest of the Sierra Nevada from Round Valley, Mono Co., California and southern Mineral County, Nevada, south to central San Bernardino County, California. (See map). The southern boundary may be roughly indicated by a line drawn from Barstow, California to Searchlight, Nevada along which line it intergrades with pyrrhus. Eastward it ranges at least to the Belted Mts., Nye County, Nevada, and Boulder Dam, Nevada; its presence beyond the Colorado River is not yet established. The following are the known localities of collection:

Nevada

Mineral County:	NYE COUNTY:
Endowment Mine, Excelsior Mts.	Grapevine Mts., above Salt Wells
Esmeralda County:	Bullfrog
7 Mi. N. of Arlemont	Near Oak Spring, Belted Range
McAfee Ranch (near Mono	(1/2 Mi. S., 1 M. S., 4 Mi.
Co. border)	SE., 1/2 Mi. NW.)
1.7 Mi. S. of Goldfield	CLARK COUNTY:
Lida	Indian Spring Valley
7 Mi. S. of Tonopah	Las Vegas Valley
	Las Vegas Wash
	Boulder Dam Site
	Harris Spring, Charleston Mts.

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MONO COUNTY: N. end Round Valley INYO COUNTY: Rocky Creek above Round Valley Birch Creek, W. of Bishop Bishop Creek $(6, 6\frac{1}{2}, 7, 7\frac{1}{2}, 9, 10, 11 \text{ and }$ 12 mi. W. of Bishop) 2 Mi. S. of Aberdeen 2 Mi. W. of Independence Independence Creek Mesquite Spring (N. end Death Valley) Beveridge Canyon Lone Pine Carroll Creek 2 Mi. W. of Jackass Spring (Type locality) Emigrant Canyon, Panamint Mts. Coso Valley Dante's View, Black Mts. Wild Rose Spring Maturango Spring

California

INYO COUNTY (continued): Junction Ranch Hanaupah Canyon, Panamint Mts. (Hananpole or Hannopee) Johnson Canyon, Panamint Mts. Goler Canyon, Panamint Mts. Near Ballarat (6 mi. S.; 7 and 10 mi. SW.) Shepherd Canyon, Argus Mts. Little Lake SAN BERNARDINO COUNTY: Slate Range, NW. of Borax Flat Willow Creek, Panamint Mts. 5 Mi. S. of Cave Spring 4 Mi. NE. of Randsburg Odessa Canyon, Calico Mts.

Near Baker

Coolgardie

Yermo

KERN COUNTY: Last Chance Canyon Near Mohave 6 Mi. E. of Brown

Lepidosis and Form.—Size medium among rattlesnakes. Scale rows at midbody usually 23 (73 per cent), occasionally 25 (25 per cent), rarely 21 (2 per cent). The scales are keeled, except the first row on each side. Ventrals: males (32 specimens), max. 181, min. 162, av. 174.44±0.50, interquartile range 171.6 —172.2, coefficient of variation 2.4 per cent; females (22 specimens), max. 182, min. 173, av. 178.72±0.40, interquartile range 176.8—180.6, coefficient of variation 1.6 per cent. Anal entire. Caudals: males 28 to 23, average of 33 specimens 25.0±0.16; females 22 to 17, average of 22 specimens 19.4±0.21. The caudals, while generally entire, may have a few at either end of the series divided.

The supralabials usually number 13 (20 per cent), 14 (33 per cent), or 15 (39 per cent); rarely 12 or 16 (4 per cent of each). The infralabials generally number 14 (38 per cent), 15 (42 per cent), or 16 (11 per cent); occasionally 13 (4 per cent), 17 (3 per cent), or 18 (2 per cent).

The rostral is usually wider than high (equal in 13 per cent) and is in contact with the prenasals, although in some cases the prenasals are sutured, thus starting the granules which are so characteristic of *mitchellii* and *pyrrhus*. The prenasals are normally in contact with the supralabials but such contact is prevented, in 17 per cent of the specimens examined, by the extension to the rostral of the small scales anterior to the pit; there is partial interference in an additional 4 per cent. The internasals (scales in contact with the rostral between the nasals, regardless of size or relative position) usually number two; owing to the splitting off of upper corners of the prenasals there is one instance of three and another of four; this out of a total of 60 specimens.

The scales on the crown anterior to the supraoculars vary from 13 to 38 and average 25.3. The minimum scale rows between supraoculars vary from 3 to 8, interquartile range 4.9 to 6.1; the average is 5.5

Supraocular sutures are highly characteristic of this subspecies; they are present in 96 per cent of the specimens. These sutures are of considerable variety; often they are whorls or longitudinal cuts, particularly at the outer edge. Sometimes these edges are rough as if pieces of scale had been broken away (text fig. 2). The nasals are divided. The loreals vary from 1 to 5, averaging 1.98; there are two in 41 per cent of the specimens, one in 37 per cent, and greater numbers in 22 per cent. The scales along the canthus rostralis, from internasal to supraocular, usually number 3, sometimes 2 or 4.

The upper preocular is divided horizontally in 4 per cent, and vertically in 18 per cent of the specimens. This is a division which is still more evident in the other members of the *mitchellii* group.

The upper preocular, which is the larger, is not in contact with the postnasal. In 46 per cent such contact is prevented by the contact of the postcanthal with the loreal, in 54 per cent by the presence of a small upper loreal.

The scale rows from labials to orbit usually number 2 or 3. Generally the third and fourth, or fourth and fifth supralabials are in contact with the pit borders; there is no conspicuous difference in size amongst the supralabials.

The first infralabials are undivided. The mental is triangular. The genials are in a single pair, relatively short and obtuse. Intergenials are present in 4 per cent of the specimens; submentals are not in evidence.

In shape the head is subtriangular, flat-topped and low. The average ratio of body length to head length in adults is 22.8.

The ratio of the length of tail to total length, exclusive of rattle, averages 0.079 in adult males and 0.059 in females.

The largest specimen examined measured 885 mm. (35 in.), the smallest 257 mm. (10 in.). A specimen 860 mm. long weighed 376 grams. The smallest female with eggs measured 674 mm.

Color and Pattern.—This subspecies is highly variable in color and pattern, as if the several desert mountain ranges which it inhabits had produced individual races. The ground color may be straw, tan, buff, yellow-brown, red-brown, gray, or blue-gray. Upon this there is superimposed a series of darker dorsal blotches which, while usually subhexagonal in shape, may approach circles, diamonds, squares, or rectangles. They are buff, gray, brown, or deep red-brown, and may, or may not, be sharply contrasting with the ground color. Some of the contrasts and harmonies, particularly in the browns, are very striking, rendering this one of the handsomest of rattlesnakes, exceeded only by *enyo* and *molossus*.

There is a secondary series of blotches on the sides; at about mid-body the main dorsal series contacts these so as to form rings, which become narrower and less sharply in contrast with the ground color toward the tail. At the neck several dorsal blotches may coalesce to form a longitudinal band. The inter-blotch areas are lighter dorsally than laterally. Anteriorly the sides are often suffused with a punctated application of gray (even on the brown specimens), a character found in *pyrrhus* as well. The dorsal blotches are sometimes even-edged, but are more often serrated by a border of unicolor scales in the manner of *scutulatus*. Sometimes the light scales bordering the blotches are conspicuously lighter than the rest of the ground color. Often the light scales, immediately anterior to the blotches, are posteriorly tipped with black; this is, in fact, quite characteristic of the present subspecies.

Northern specimens are darker and more conspicuously and definitely marked than those from the south; the latter more nearly approach the amorphous punctations of *pyrrhus*. Red-brown or dark-brown specimens are the rule from the northwestern corner of the range in the vicinity of Bishop Creek, California. In the northeastern corner, in Nevada, blues and grays predominate. The southeastern specimens are generally tan, blotched with brown.

The ventral surface is usually buff or tan, with aggregations of darker punctations.

The head is spotted, but less conspicuously and regularly than the body. Supraocular light cross-marks are usually absent, but the outer edge of each supraocular may be light. There is often a dark dash from the eye to a point above the corner of the mouth, but in many specimens this is obscured by a characteristic suffusion of gray, which, in the tan or brown specimens, is in rather sharp contrast with the dorsal color.

The tail rings are usually distinct, but the last two or three, which are generally black and in strong color contrast with the rest of the body, are not evenly outlined, and may be partly confluent.

The body blotches vary in number from 30 to 43, the average being 37.0. The tail rings number 6 to 9 (average 6.8) in the males, and 3 to 6 (average 4.6) in the females.

CHARACTER SUMMARIES

Having presented separately, for each of the three subspecies of *mitchellii*, the essential details of lepidosis, form, and appearance, I deem it desirable to combine the enumerations of other characteristics, in order to avoid repetition under each subspecies, since the differences between the three forms are not considerable.

Habitat.—All three subspecies of *mitchellii* are essentially rock-dwelling snakes, and to a large extent, but not entirely, are restricted to the wastes of the southwestern deserts. Here, however, they are not universally distributed; from the level, sandy plains and the great alluvial fans they are generally absent, their habitat being in the rocky mountains and buttes which rise above the plains. Thus, while the range of *mitchellii* is roughly coincident with those of *C. cerastes*, *C. scutulatus*, and *C. atrox* in parts of Arizona and California, they are not particularly active competitors, for locally there is often a rather sharp distinction in the habitat which each species prefers.

For example, in the Panamint and Death Valley regions we find *stephensi* in the lava flows, rocky buttes, and the mountains themselves (to altitudes of at least 7000 ft.) rather than in the plains between, the latter being inhabited by *cerastes*. In the Mohave Desert we find *cerastes* and *scutulatus* on the flats,

and *pyrrhus* in the mountains, and the same is true in southwestern Arizona where *atrox* is included with the plains species. From the Imperial and Coachella Valleys *pyrrhus* seems absent, although present in all the surrounding mountains.

In the Peninsula ranges of southern and Lower California, including the San Bernardinos, San Jacintos, Cuyamacas, Sierra de Juarez, and Sierra San Pedro Mártir, we find *pyrrhus* ranging into Upper Sonoran habitats and even touching Transition. Yet, in the chaparral and oaks, it continues to show its preference for rocky outcrops, although not restricted to them. Here it reaches altitudes of at least 5300 ft. in areas shared with *Crotalus ruber* and *C. c. oreganus*. But while the latter are equally common westward to the ocean, *pyrrhus* rarely is found below the 1200 ft. contour on the coastal slope.

It is in these mountains also that *mitchellii*, in the subspecies *pyrrhus*, reaches its maximum mainland size, specimens slightly exceeding 1220 mm. (48 in.) having been accurately measured. Such an individual would weight about $2\frac{1}{2}$ lb. (1130 g.). This size is not approached by either *stephensi* or *m. mitchellii*.¹³ These, of course, are exceptional specimens; I would consider 1100 mm. (43 in.) as representing a "large" adult male *pyrrhus* in the foothills of San Diego County. In Arizona and, in fact, throughout the truly desert areas, this size is not reached, few adults exceeding 920 mm. (36 in.). The Angel de la Guarda Island specimens are very large, reaching at least 1240 mm. (49 in.). *Stephensi* is a smaller snake than *pyrrhus*, specimens exceeding 850 mm. (33¹/₂ in.) being exceptional. *M. mitchellii*, while smaller than *pyrrhus*, sometimes exceeds 900 mm. (35 in.) and one specimen 939 mm. (39 in.) has been noted. However, most of the adult males run about 850 mm. (33¹/₂ in.) in length.

From a few areas we have some statistics as to the relative frequency of occurrence of *mitchellii* compared with the other species with which it shares the range. Thus, in four lots of rattlers brought up from the vicinity of Cape San Lucas there were 69 *m. mitchellii* or 17.6 per cent, out of a total of 391 rattlers; 6.4 per cent were *enyo*, the rest being *lucasensis*.

In San Diego County, out of 2006 rattlesnakes recorded, only 260 or 12.6 per cent were *pyrrhus*, for this form was greatly exceeded in number by *ruber* and *oreganus*.

Along the line of the Santa Fe Ry. between Hillside and Wickenburg, Yavapai County, Arizona, a collection of 454 rattlers yielded 19 *pyrrhus* or 4.2 per cent. The majority were *atrox* and *scutulatus* (55.6 and 31.9 per cent) with a few *molossus* and *oreganus* (4.6 and 3.7 per cent). Since these specimens were collected by track maintenance crews it is to be expected that the rock inhabiting forms would not be as well represented as those preferring the flat-lands.

Thus, it is seen that where *mitchellii* is in competition with other forms it usually constitutes only a small part of the rattlesnake population. Several species of rattlers occur in most of the territory inhabited by *pyrrhus* and *mitchellii*

 $^{^{13}}$ A specimen (USNM 64588) 1295 mm. (51 in.) long is contained in the National Museum. The locality of collection is uncertain, but it is recorded tentatively as Cedros Island. This I rather doubt, since subsequent collectors have failed to find it there, although other rattlers (*C. exsul*) are not uncommon.

although they may have the rocky prominences to themselves. *Stephensi*, on the other hand, is the sole possessor of most of its range, or, at least, shares it only with *cerastes*, with which it is hardly in competition, so clearly does the one prefer valleys and sand, and the other rocky slopes and mountains.

There is evidence that where *mitchellii* shares its territory with others it does not den with them. Thus, a reliable observer reported having seen some twenty *pyrrhus* in a shallow cave under a large granite boulder in San Diego County; there seemed to be no other rattlers present, although both *ruber* and *oreganus* are more common than *pyrrhus* in that particular place. In another instance, in December, nine rattlers were found under a single stone; all were young adult *pyrrhus*.

Breeding.—Specimens of stephensi have been noted with 6 and 8 eggs; pyrrhus with 3, 4 (2 specimens), and 5. Experience with other species leads us to believe that these pyrrhus broods were smaller than the average for the species.

Habits.—In the field *pyrrhus* is a distinctly more nervous species than *ruber*; rather it resembles *oreganus* in its alert readiness to defend itself or escape. It will usually rattle if alarmed. Mrs. G. O. Wiley, however, reports it as easily tamed as other species, if not more so.

As is the case with most of the western rattlers, particularly the desert forms, mitchellii is largely nocturnal, especially in summer. However, it will be found abroad in the daytime in spring, and to a less extent in autumn. Thus, a specimen of stephensi was seen to issue from a hole at 6:30 p. m., in August. In late March specimens were observed crossing the road at Bullfrog, Nevada, at 3:00 p. m., and near Ballarat, at 6:25 p. m. In the spring, in San Diego County, specimens of pyrrhus have been observed sunning themselves before rock clefts in which they took refuge so promptly as to indicate advance consideration of these retreats.

Food.—The snakes of the mitchellii group, as is usual with the larger rattlesnakes, subsist principally upon rats, mice, and other small mammals. Amongst these, *Dipodomys* has been recognized. Young specimens are probably more accustomed to lizards, and even the adults do not scorn this prey. Amongst the species noted in the stomach contents were *Uta stansburiana*, *Cnemidophorus tessellatus*, and *Eumeces skiltonianus*. One large specimen contained both mammal hair and a *Uta*. One large *mitchellii* was observed to eat a ground squirrel which had been shot some three hours before.

Birds are eaten occasionally. Thus Mr. Dean E. Batchelder informed me he had found 8 birds, presumably goldfinches, in the stomach of a *pyrrhus*. All had been swallowed head first. This was near an aqueduct construction camp where a lawn, garden, and bird bath had been installed on the desert 10 miles north of Desert Center, Riverside Co., Calif. Birds had been attracted from great distances and evidently the snake had lain in wait for them.

Hemipenes.—The hemipenes of the mitchellii group may be described thus: Completely bifurcate with divided sulcus. Base covered with short, stiff spines, particularly at the outer shoulders; the branches covered with reticulate fringes. There is a sharp cleavage between spines and fringes (a characteristic of *Crotalus* as compared with *Sistrurus*, with the partial exception of *C. lepidus*). The apices are calyculate. In shape the two lobes are of medium weight (ratio of length to diameter about 2.6) similar to the *confluentus* group; this is in contrast to the attenuated organs which characterize the *atrox* group, or the opposite extreme, illustrated by the short heavy lobes of *molossus*. The spines cannot be counted with accuracy, since they vary by imperceptible degrees from mere pustules to full points. The fringes vary from 27 to 34, averaging about 31.

One of the important variations in the hemipenes of *Crotalus* is the presence or absence of spines in the crotch between the lobes. These spines are present in all subspecies of *mitchellii*. They are especially conspicuous in *mitchellii mitchellii* and *stephensi*, somewhat less so in the intermediate specimens (*pyrrhus*) from California, and are least perceptible in *pyrrhus* from Arizona.

Fangs.—The fangs of *mitchellii*, in shape and size, follow closely the *confluentus* group, that is, they are shorter proportionately than those of *terrificus*, *adamanteus*, and the *atrox* group. Average adult ratios of body and head length to fang length (measured from the lower edge of the upper lumen to the tip) are as follows:

Fang	Length	Ratios
------	--------	--------

	L/F	H/F
Mitchellii	151	5.74
Pyrrhus	107	5.01
Stephensi	128	5.59

Here again we have a substantial difference between *mitchellii* and *pyrrhus*, although one which is obviously correlated with proportionate head size.

Venom.—The physical characters of the venoms of these three subspecies are indicated in the following table:

	Mitchellii	Pyrrhus	Stephensi
Specimens milked	64	298	13
Average yield dry venom per adult snake, mg.	33	215	73
Maximum vield, mg.	75	350	129
Specific gravity	1.078	1.090	1.088
Average MLD	0.04?	0.50	0.20

The MLD is taken from data kindly furnished by Dr. Thos. S. Githens of the Mulford Biological Laboratories of Sharp and Dohme, and represents the fatal dose for a pigeon of 350 g. weight. From results in other species we would expect *mitchellii*, with its small head and short fangs, to have a relatively powerful venom, as compared with *pyrrhus.*¹⁴

Rattles .- Studies, as yet unpublished, indicate that the characteristics, and

¹⁴ Githens (Journal of Immunology, Vol. 29, p. 171, Aug. 1935) reports two qualities of *mitchellii* venom: a "strong" with an MLD of 0.04 and a "weak" with an MLD of 0.50. The venoms which yielded these results were sent to the biological laboratory from San Diego. Through correspondence with Dr. Githens I have ascertained the lot numbers involved in the several assays and checking the original data I find that three assays yielding an average MLD of 0.50 contained only *pyrrhus* venom. One assay resulting in an MLD of 0.04 was based exclusively on *mitchellii* venom. Only one assay tends in any way to upset the theory that the venoms of *pyrrhus* and *mitchellii* differ considerably, the latter being the more toxic. This assay, on a mixture of *mitchellii* and *pyrrhus* venoms sent in before the subspecies were distinguished, also yielded an MLD of 0.04, whereas some figure between the two might have been expected. I am unable to explain this unless the more powerful venom tends to mask the weaker.

particularly certain measurements, of the rattles, are of considerable interest in classification. These dimensions are found to be quite consistent, and from them it is possible to verify relationships and differences. As an instance, the width of each rattle (where the string is complete and the rattle-number in the sequence is therefore known) is found of value in classification. In the present study we have the following data:

AVERAGE WIDTH OF RATTLE IN TENTHS OF MILLIMETERS

RATTLE NO.	1	2	3	4	5	6	7	8	9
Mitchellii	82	99	111	127	136	144	148	147	146
Parrhus (Col)	70	83	96	109	122	131	128	139	138
Durrhus (Ariz)	62	76	91	103	111	120	136	138	140
Stabbouci	48	61	75	103	112	116			
Stephensi	40	01	//	107					

The figures are not particularly trustworthy beyond the fifth rattle for two reasons; first, a sufficient number of specimens is not available to afford accurate averages; and, secondly, sexual dimorphism begins to affect the result beyond the sixth rattle, and therefore for accuracy of diagnosis it is necessary to treat the sexes separately. However up to the sixth rattle, except in the case of *stephensi*, of which comparatively few specimens, even of the first rattles, are available, the figures are quite reliable. These studies, to be presented elsewhere, show that, within geographically homogeneous groups, the coefficient of variation of the rattle widths of the first five rattles usually runs from 5 to 7 per cent and rarely exceeds 9 per cent. Under such circumstances differences such as those indicated in these tables, particularly between *mitchellii* and *pyrrhus*, can be shown mathematically to be highly significant.¹⁵

While it is not believed advisable to attempt any species differentiation exclusively based on rattle divergences, these certainly should not be neglected as confirmatory evidence.

RELATIONSHIPS AND DIFFERENCES

As I have stated before, *mitchellii* cannot always be distinguished from the other rattlesnakes by its best known character, namely, the separation of the rostral from the prenasals by small scales or granules; for this character is not universally positive in either of the southern races, *m. mitchellii* and *pyrrhus*, and it is always negative in *stephensi*. Furthermore, this prevention of contact is of sporadic occurrence in other forms, particularly in *oreganus* from central Arizona. Nor is the depression of the head, while somewhat evident, the clear-cut and obvious character which it has been occasionally considered in the past. The same is true of the shape of the rostral, which is not always wider than high.

In general, it can be said that these snakes are conspicuous amongst the rattlesnakes for the tendency to subdivision of certain head scales (prenasals, canthals, loreals, and preoculars in *mitchellii* and *pyrrhus;* and supraoculars in *stephensi*), and for the punctated application of color and pattern. Yet there is sufficient variation and divergence in all of these characters so that simple and invariable keys are impossible; therefore, considerable judgment and some experi-

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¹⁵ Employing the usual formula for significance by evaluating the ratio which the difference between the means bears to the standard error of the difference.

ence are necessary in their application if errors are not to be made. However I do not think that this is an adverse criterion of the validity of these forms, since the summation of the differences is impressive; and some differences which are not particularly useful as key characters, such as the form of the hemipenes, nevertheless are important in the final determination of validity.

The nearest existing relatives to *mitchellii* are *tigris*, *cerastes*, and *confluentus* (the latter through the subspecies *oreganus* and *lutosus*), probably in the order named. These affinities are shown in form, scalation, pattern, and hemipenes, as will be pointed out.

The characters of lepidosis which are usually employed statistically in distinguishing species of snakes, are not of particular value in separating the members of the *mitchellii* group, either from each other or from some of their near relations, for a number of rattlers, including the several subspecies of *confluentus* and *mitchellii*, as well as *scutulatus* and *tigris* do not differ greatly in these characters. However, a few tendencies are to be noted.

In scale rows, 25 is the mode in *m. mitchellii* and *pyrrhus*, but this is reduced to 23 in *stephensi*, which, in this particular, resembles *tigris*. About half of the Arizona specimens of *pyrrhus* have 23 scale rows, a much higher percentage than is encountered in the California specimens.

Mitchellii is a rough-scaled species, the dorsal scales being sharply ridged and with raised bosses posterior to the middle of each scale. The latter are more conspicuous in *mitchellii mitchellii*, and in southern California *pyrrhus*, than in *pyrrhus* from Arizona or *stephensi*. However, in none of these snakes are the bosses so extreme as in *cerastes*, which is outstanding in this character amongst our southwestern rattlers; and even this form is exceeded in the prominence of these dorsal scale protuberances by *durissus*. The extreme spinal ridge of *durissus* is also absent in *mitchellii*, *enyo* most nearly approaching the tropical rattler in this character.

In ventrals *mitchellii* and Arizona *pyrrhus* average slightly lower than California *pyrrhus*, but the difference is not conspicuous; *stephensi* is also low. In this character *tigris* is conspicuously different from *stephensi*, as set forth in the following table:

AVERAGE VENTRAL SCALE COUNTS

	Males	Females
Mitchellii	176.7	179.5
Pyrrhus (Southern California)	178.3	180.0
Pyrrhus (Arizona)	174.4	175.4
Stephensi	174.4	178.7
Tigris	165.2	168.5

The extent of the difference between *stephensi* and *tigris*, as indicated by the ratio of the difference between the means to the standard error of the difference, is 9.2 for the males and 9.3 for the females. In calculations of this kind any ratio above 3 is usually considered significant; 9 may be taken as conclusive on this point, that is to say the difference is real and cannot be attributed to chance differences in sampling. The differences in caudal scale counts are not important; *stephensi* and *mitchellii* are slightly higher than *pyrrhus*.

It is interesting to note that there is less sexual dimorphism in ventral scales

in *mitchellii* than is apparent in most rattlesnake species. In the *mitchellii* subspecies the females average about 3 more ventrals than the males; the *confluentus* group and many other rattlers run from 4 to 7.

In labial counts we find *pyrrhus* somewhat higher than *mitchellii*, which, in turn, exceeds *stephensi*. None of the differences is sufficient to be of interest as a key character.

Divided first infralabials are quite characteristic of Arizona *pyrrhus*, being present in 70 per cent of the specimens; in California *pyrrhus* they are frequent in San Bernardino County but are rarely met with elsewhere in the range of *pyrrhus*, or in *mitchellii* or *stephensi*. Intergenials and submentals are occasionally noted, but are not characteristic of any of these forms.

Of the other head scales, such as the internasals, canthals, inter-supraoculars (frontals), nasals, loreals, and oculars, whose numbers, contacts, and arrangements are so frequently of value in rattlesnake diagnosis, we can in the *mitchellii* group make little use because of their tendency to be split to such a degree that their classification becomes impossible. For instance, where there is so frequently a row of scales between prenasal and rostral (as in *mitchellii* and *pyrrhus*) the internasals are indeterminate; canthals and loreals cannot be separated; preoculars are broken vertically, horizontally, or both (text fig. 1), and thus are confused with loreals. But a few differences of importance may be noted in these scales which may be summarized as follows:

1. Supraocular sutures (text fig. 2) are highly characteristic of *stephensi* and will serve to differentiate this form from *tigris*, and, to a lesser extent from *lutosus*. Stated statistically we have the following:



Fig. 1. Crotalus mitchellii mitchellii. Lateral view of head showing subdivision of preoculars, loreals, and supralabials.

Fig. 2. Crotalus mitchellii stephensi. Dorsal view of head showing supraocular sutures.

Fig. 3. Crotalus mitchellii pyrrhus. End view of head showing absence of contact between rostral and prenasals.

	Sup	RAOCULAR	SUTUR	ES	
	(two	counts per	specime	en)	
			With	Without	
			Sutures	Sutures	Doubtful
Stephensi			120	2	2
Tigris			0	82	2
Lutosus (Cal	. and I	Nev. only)	26	168	4

Supraocular sutures are not infrequent in *mitchellii* and *pyrrhus;* they are quite prevalent in specimens from northern Baja California.

2. Internasals are determinate in *stephensi* and will distinguish this form from *lutosus*. Thus in 60 specimens of *stephensi*, one had 3 and one had 4 internasals; all others had 2. On the other hand, in 103 specimens of *lutosus* from California and Nevada there were only 4 specimens with less than 3 internasals, the complete score being as follows (the first number indicating the number of internasals, the second the number of individuals): 1/1, 2/3, 3/28, 4/62, 5/6, 6/3. Only California and Nevada specimens of *lutosus* were used in this comparison, instead of snakes from all areas, upon the theory that the former, occupying a territory close to that of *stephensi*, are the ones most necessary to differentiate from *stephensi*. It may be of internasals) are from near *pyrrhus* territory and have an increased number of internasals by reason of the splitting of the prenasals (a characteristic of *pyrrhus*), rather than of the internasals themselves, as in *lutosus* and all the *confluentus* group.

3. The rostral-prenasal interruption (text fig. 3), while not a universal key character to *mitchellii* and *pyrrhus* as was once supposed, is, nevertheless, usually indicative. Thus, it is positive in 97 per cent of *mitchellii*, and about 88 per cent of *pyrrhus*. Most of the aberrant specimens of *pyrrhus* occur in southern California, approaching the territory of *stephensi*; this is to be expected in view of the intergradation of the two forms. In *stephensi* there are no cases of the failure of the rostral prenasal contact, and the same is true of *tigris*. The interruption of this contact, thus shown to be characteristic (but not universally so) of *mitchellii* and *pyrrhus*, does occur in some other species, particularly the subspecies of *confluentus*; it is most prevalent in *oreganus* from central Arizona, where about 12 per cent of the specimens have this contact interrupted. Lack of contact has also been observed in *abyssus* and in California *oreganus*.

4. It is characteristic of all the *mitchellii* subspecies and *tigris* that the rostral is wider than high; the contrary is usually true in all the *confluentus* subspecies. However, the two dimensions are not infrequently equal, especially in specimens of *pyrrhus* from southern California, so that at best this is but a confirmatory character. Occasionally specimens of *pyrrhus* have the rostral higher than wide.

The great variability in pattern and color of all subspecies of *mitchellii* renders these characteristics of little use in classification. Outstanding are the punctulate application of color in *mitchellii* and *pyrrhus* and the indefiniteness of the pattern; the gray suffusions on the lateral areas of *stephensi* and northern *pyrrhus*; the black posterior scale tips in many *stephensi* and some *pyrrhus*; the *scutulatus* type of tail rings in many specimens of *pyrrhus* and *mitchellii*. But none of these characters is the sole possession of *mitchellii* subspecies; even the punctations are seen to be highly developed in *tigris, atrox* (although in a different manner), *confluentus* from New Mexico (Cope's *pulverulentus*), *triseriatus*, and others.

In number of body blotches and tail rings both *pyrrhus* and *mitchellii* fall below *stephensi*, and this, in turn, below *tigris*. However, the dispersion of these characters is so great that they are not useful as keys.

Coming now to form, we observe that *pyrrhus* is a somewhat heavier bodied snake than the other two subspecies. Proportionately it has a slightly shorter tail than either *mitchellii* or *stephensi*. But none of these is conspicuously different from the *atrox* or *confluentus* groups.

It is in head size that really important differences amongst the *mitchellii* subspecies are evident; here we have probably the most essential divergence between *mitchellii* and *pyrrhus*, and this in a character which must be presumed to be relatively stable.

The determination of the statistical significance of differences in such a character as the ratio of the head to body length is a somewhat involved problem. Such an investigation has been made, but its exposition would be out of place at this point, and is reserved for future publication. The conclusions concerning rattlesnakes may be summarized as follows:

1. The relationship of the size of the head to the body conforms closely to a linear equation of the form H=a L+b, the constants a and b being different for each of the several species or subspecies.

2. Owing to the presence of the constant term b in the regression equation, the ratio of body length to head length is not constant throughout life; young rattlesnakes have proportionately larger heads than adults.

3. There is a close correlation between head and body size in any one form, the coefficient of correlation probably being about ± 0.85 to 0.90. The dispersion about the regression line approximates the normal curve of error. The dispersion remains nearly proportional throughout life, although increasing slightly with age. The coefficient of variation about the regression line is from 2.5 to 3.5 per cent in homogeneous groups.

To simplify the problem in the present instance we can restrict our investigation to adult groups of approximately the same body size; if this be done the constant term b may be neglected, since the ratio L/H will be practically constant for each subspecies in any short length-range. The results of such a study of restricted adult groups are as follows, all specimens having been measured under the same conditions of preservation:

Adult Head-Length Ratios

		Length	Length	Head Length	
	Number of	Range	Average	Average	Ratio
	Specimens	mm.	mm.	mm.	L/H
Mitchellii	46	725_915	784	31.9	24.6
Pyrrhus (Calif.)	41	720_932	815	37.9	21.5
Pyrrhus (Ariz.)	14	700_895	775	35.9	21.6
Stephensi	20	720-872	783	34.4	22.8
Tigris	22	577_770	673	26.4	25.6

Thus it is seen that there is an essential difference in this character (which our investigations lead us to consider stable and consistent) between *pyrrhus* and *mitchellii*, and between *stephensi* and *tigris*. It will be noted that the average size of the specimens of *mitchellii* is slightly less than the average for California *pyrrhus*, and the *tigris* average is less than *stephensi*. Since L/H increases with growth, if the average length were the same in the two cases the differences in the L/H ratios would be slightly greater than is shown in the table.

As a further proof of the difference between *mitchellii* and *pyrrhus* the regression lines for the L—H relationships were determined; all specimens were reduced to the same standard body size and the hypothetical head length for each specimen was calculated on the assumption that the deviation of any individual from the regression line for that subspecies remains constant (in percentage) throughout life. By this method it was determined that the ratio of the difference in the means of the head sizes to the standard error of the difference was over 17, which indicates that the difference is a real one and not attributable to the accidental composition of the group available for study (i. e., sampling errors). On the other hand between Arizona and California *pyrrhus* there was found to be no significant difference, the corresponding ratio being only 0.4.

Tigris has proportionately the smallest head amongst all the rattlesnakes; it is of interest to note that it is closely approached by *mitchellii*; on the other hand *pyrrhus* and *stephensi* approximate the rattlesnake mode in the body-head ratio.

That these differences in the head dimensions between *mitchellii* and *pyrrhus*, and between *stephensi* and *tigris* are not merely an exaggeration of a minor statistical deviation will be at once apparent to any one having the opportunity to compare adult specimens of these forms in life. It is to be remembered that there are proportionately similar differences in head width and in depth as well as in length; there is therefore a difference in bulk approximately equal to the cube of any linear dimension. The result is so striking that there is no difficulty in segregating these forms at a glance when adults of approximately the same body length are available.

As might be expected, fang length is closely correlated with head length¹⁶ and thus the fangs repeat the differences observed in the ratio of head size to length of body overall. But here we find that the differences are even more impressive, for *tigris* and *mitchellii* not only have shorter fangs than *stephensi* and *pyrrhus* because of their smaller heads, but have, in fact, fangs which are disproportionately shorter even where snakes of the same head size are taken. With relation to the body lengths overall, the discrepancy is still greater. This is apparent from the following table showing data for the subspecies under consideration and their relatives:

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	L/F	H/F		L/F	H/F
Mitchellii	151	5.74	Tigris	165	6.11
Pyrrhus	107	5.01	Lutosus	131	5.49
Stephensi	128	5.59	Cerastes	98	4.83
(L = body-le	ength over	all; $H = 1$	ength of head; $F =$ length of fang	, upper	lumen
to point).	-		· · · · ·	••	

¹⁶ The regression equation is of the form F = a H - b.

The resemblance of *mitchellii* to *tigris* rather than to *pyrrhus*, and of *stephensi* to *lutosus* rather than to *tigris* is at once evident.

Venom differences, at present imperfectly known, have already been set forth. I would anticipate that *mitchellii* would again show an affinity to *tigris* rather than *pyrrhus*, but its MLD has only been tentatively determined. Githens reports *tigris* venom to be the most toxic of any of the 22 subspecies of rattlers thus far investigated.

The study of the rattles of the rattlesnake, from the standpoint of species differences is so involved that publication of these data must be reserved for another place. Suffice it to say that *mitchellii* is well differentiated from *pyrrhus*. *Tigris* more nearly resembles *pyrrhus* than *stephensi*. *Mitchellii* has the largest rattles of any known rattlesnake, up to and including the fifth rattle, a most surprising fact in view of its relatively small size. It considerably exceeds its relative *pyrrhus* and is in fact approached most closely by *adamanteus* and *lucasensis*. The first of these being the largest of rattlesnakes, its possession of large rattles is not unexpected.

The hemipenial characteristics of the *mitchellii* group afford the clearest differentiation from the *confluentus* group, for although both of these have organs of somewhat the same ratio of lobe length to diameter (thus sharply different from the attenuated organs of the *atrox* group on the one hand and the globular habitus of *molossus* on the other) the *confluentus* group is without spines in the central crotch while these are always present in the *mitchellii* group. Here *pyrrhus* shows a closer affinity to *lutosus* and *oreganus* than do *mitchellii* or *stephensi*, for the latter have patches of spines in the cleft while in *pyrrhus* (especially those from Arizona) the spines in this area are usually few and not particularly large. In this character *tigris* resembles *stephensi*; *cerastes* also has a cleft-patch.

ISLAND SPECIMENS

The following Gulf of California island specimens are available for study:

Angel de la Guarda	5
San José	1
Espiritu Santo	3
Ceralvo	1

It is interesting to survey these for indications of incipient differentiation from the mainland forms, although there are not sufficient specimens upon which to premise descriptions of new species unless the differences be very wide.

First, we find, based on the most important difference (head proportion), between *mitchellii* and *pyrrhus*, that the Angel de la Guarda specimens are *pyrrhus*, while those from San José and Ceralvo are *mitchellii*, which is quite what would be expected geographically. The Espiritu Santo specimens are between the two mainland forms, although somewhat nearer *mitchellii* than *pyrrhus*; in rattle dimensions they are somewhat closer to the latter, but for the present we will consider them as *mitchellii*. In ventrals the Angel de la Guarda specimens are distinctly higher than most of the specimens of *pyrrhus*, while those from the other islands have fewer scales than the average of *mitchellii*. There are indications that both differences would be significant, were enough specimens available to determine the dispersions of the island specimens more accurately. The caudals show no deviations of interest. The labials are rather low in the Angel de la Guarda specimens, and supraocular sutures are prevalent, showing in this last character an affinity for the specimens from the mountains of Lower California.

The Angel de la Guarda specimens are very large; they are pink or straw and usually have black scale tips; in color they resemble Arizona specimens rather than those from California. It is quite possible, I think, that USNM 64588, the largest known *pyrrhus*, may have come from Angel de la Guarda instead of Cedros Island, as has been presumed.¹⁷

The other island specimens are also pink, with the exception of that from Ceralvo, which is gray. We conclude that these island forms have been so long separated from the mainland that differentiation has begun, but it is not sufficient to permit taxonomic separation, at least not until much larger series are available.

It is unfortunate that the type specimen of *mitchellii* (USNM 5291¹/₂) has been lost and that Cope did not give the head measurement. He records this snake as being 44 in. (1118 mm.) long, which is so much larger than any other specimens from the Cape that we are disposed to doubt the accuracy of the locality. As was so often the case in those days the specimen was probably recorded from the locality from which it was sent, rather than the point of collection. The color and pattern descriptions also do not fit *mitchellii*.

We know from the tail length that the specimen was a male. The ventral scale count, given as 198, is so much higher than any other Cape male specimen (max. 181) that the specimen was either a freak or there has been a miscount. Calculations indicate an extremely small chance of such a high count, assuming that the dispersion follows the normal curve of error (which other studies indicate to be the case), for the deviation of this specimen is over six times the standard deviation. We conclude that the derivation of this specimen from Cape San Lucas is exceedingly doubtful, and if all the facts were known a shifting of names might be necessary.

CONCLUSIONS

Crotalus mitchellii is a valid species of rattlesnake containing three well differentiated subspecies. C. m. mitchellii, C. m. pyrrhus, and C. m. stephensi. Of other existing species their closest relatives are C. tigris, C. cerastes, C. c. oreganus, and C. c. lutosus. C. m. mitchellii shows an affinity to tigris; while pyrrhus and stephensi have important resemblances to oreganus and lutosus.

¹⁷ Schmidt, 1922, p. 700.

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Fig. 1. *Crotalus mitchellii mitchellii*. San Lucan Speckled Rattlesnake. Adult male, collected at La Rivera, Baja California, by C. C. Lamb.



Fig. 2. *Crotalus mitchellii pyrrhus*. Southwestern Speckled Rattlesnake. Adult male, collected at Yaqui Well, San Diego County, California, by E. E. Benson. .



Fig. 1. Crotalus mitchellii pyrrhus. Southwestern Speckled Rattlesnake. Adult male, collected in Tinajas Altas Mts., Yuma Co., Arizona, by Dr. C. T. Vorhies.



Fig. 2. Crotalus mitchellii stephensi. Panamint Rattlesnake. Adult male, collected 2 mi. S. of Aberdeen, Inyo Co., California, by F. E. Walker.

